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EOCENE OF CENTRAL WYOMING. PART 9.
THE OLDEST KNOWN HYSTRICOMORPHOUS
RODENT (MAMMALIA: RODENTIA)

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ABSTRACT

The rostral portion of the skull of a new genus and species of rodent, *Armintomys tullbergi*, from the earliest middle Eocene of the Wind River Basin, Wyoming, provides the geologically oldest known record of the hystricomorphous zygomasseteric structure. *Armintomys* also preserves the oldest known occurrence of incisor enamel that is transitional from pauciserial to uniserial. Other dental characters include: anteriorly grooved incisor, small premolars and relatively primitive sciuravid-like molars.

Analysis of this unique combination of characters implies that *Armintomys* is the oldest known myomorph rodent and the only known representative of a new family, Armintomyidae, which is referred, with question, to the myomorph superfamily Dipodoidea. *Armintomys* is more primitive, especially in premolar retention and structure, than the Bridgerian zapodid *Elymys* from Nevada, but adds to evidence from the latter for an early origin and radiation of dipodoid rodents.

INTRODUCTION

A recurring theme in rodent evolution has been modification of the skull, jaws, and masseteric musculature so as to move the origin of the muscles anteriorly for more efficient chewing and gnawing. Hystricomorphy, one such modification, involves enlargement of the infraorbital foramen for transmission of part of the masseter medialis muscle from an origin on the rostrum anterior to the zygoma. Hystricomorphy has been considered a character of systematic importance; it was one of the diagnostic features of Waterhouse's (1839) Hystricina and Brandt's (1855) Hystricomorphi.

In his superb monograph on rodent morphology and phylogeny, Tullberg (1899) observed that hystricomorphy occurs in both of his major rodent subdivisions, the Hystricognathi and the Sciurognathi. This recognition led to current opinion that hystricomorphy has developed a number of times among rodents. As Wood (1985:480) wrote, "I believe that hystricomorphy, among these groups, developed independently at least seven and possibly as many as ten or twelve times, as parallelisms." According to the fossil record, hystricomorphy first appears in at least six groups of rodents in the middle and late Eocene (Table 1). The transition from protrogomorphy (origin of masseter entirely on zygoma), the primitive con-

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Table 1.—*Appearance of hystricomorphy in Eocene rodents.*

Taxon	Geographic record		Geologic record		Reference
	North America	Wind River Basin, Wyoming	Gardnerbuttean, early middle Eocene	This paper	
<i>Armintomys tullbergi</i>	North America	Wind River Basin, Wyoming	ca. 49–50 ma	Wood, 1977	
<i>Prolapsus</i>	North America	Whistler Squat, Texas	Early Uintan, late middle Eocene ca. 46–47 ma		
<i>Protoptychus</i>	North America				
<i>P. hatcheri</i>	North America				
<i>P. ?smithi</i>	North America				
<i>Simimys</i>	Uinta Basin, Utah		Early Uintan, late middle Eocene ca. 46–47 ma	Scott, 1895 Wahlert, 1973	
	Washakie Basin, Wyoming				
	North America				
	southern California		Late Uintan-Duchesnean, late Eocene ca. 44–38 ma	Wilson, 1949 Lindsay, 1977 Emry, 1981	
<i>Protadelomys</i> (and other Robiacian and later theridomorphs)	Europe			Hartenberger, 1968 Wood, 1974	
<i>Tamquammys</i> ¹	Egerkingen, Switzerland			Dawson <i>et al.</i> , 1984	
	Inner Mongolia		(probably equivalent to early Uintan), late middle Eocene, ca. 46–47 ma		
<i>Saykanomys</i>	Kazakhstan				
	Mongolia		Late Eocene	Dawson <i>et al.</i> , 1984	
	Kazakhstan		ca. 44–38 ma		
<i>Petrakozlovia</i>	Mongolia		Late Eocene	Dawson <i>et al.</i> , 1984	
	Kazakhstan		ca. 44–38 ma		
<i>Yuomys</i>	China		Late Eocene	Dawson <i>et al.</i> , 1984	
			ca. 44–38 ma		

¹ Asian correlations not exact.

dition, to hystricomorphy can be traced in the Eocene fossil record of two families, the Cocomyidae and the Theridomyidae.

The new, early middle Eocene (Gardnerbuttean) hystricomorphous rodent described here provides the earliest known record of hystricomorphy. It is also the earliest known rodent to show modification in structure of the incisor enamel, which is transitional from pauciserial to uniserial. This character too has systematic implications.

Land Mammal Age terminology and usage follow Woodburne (1987) for North America, and Savage and Russell (1983) for other areas. Abbreviations include: CM, The Carnegie Museum of Natural History, Pittsburgh; AMNH, American Museum of Natural History, New York; YPM, Yale Peabody Museum, New Haven; L, length; W, width; ma, million years; mm, millimeters; m, meters.

SYSTEMATICS

Suborder Myomorpha

Superfamily ?Dipodoidea

Family *Armintomyidae*, new family

Diagnosis.—Rodents with hystricomorphous zygomaseteric structure, incisor enamel pauciserial leading to uniserial; brachydont cheek teeth including P^{3-4} , M^{1-3} ; P^3 small; molars longer than wide, with well-developed hypocone, weak lophs.

Included genera.—*Armintomys*, n. gen.

Armintomys, new genus

Type species.—*Armintomys tullbergi*, n. sp.

Known distribution.—Early middle Eocene (Gardnerbuttean) of Wyoming.

Diagnosis.—Infraorbital foramen wide and high; depression marking origin of masseter medialis extending forward from maxilla onto premaxilla, slightly anterior to suture with maxilla. Upper incisor with one groove. P^3 small peg; P^4 probably short anteroposteriorly; M^{1-2} longer anteroposteriorly than wide, with mesostyle, low lophs, hypocone nearly as well developed as protocone.

Etymology.—*Arminto*, from Arminto, Wyoming, the major settlement near the locality; and *mys*, Greek for mouse.

Armintomys tullbergi, new species

(Fig. 1–5, Table 1)

Holotype.—CM 47220, partial skull with incisors, left P^3 , M^{1-2} .

Hypodigm.—Holotype only.

Horizon and locality.—CM loc. 1548, Lost Cabin Member, Wind River Formation, Wind River Basin, Natrona County, Wyoming.

Age and known distribution.—The holotype and only known specimen of *Armintomys tullbergi* was found on the surface of a 6.2 meter-thick gray mudstone, which is interpreted as an overbank/paleosol deposit (Stucky, 1984). CM locality 1548 occurs stratigraphically in the upper gray sequence of the Lost Cabin Member of the Wind River Formation. Its fauna (17 mammalian species) is used to define the *Palaeosyops borealis* Assemblage Zone, which is Gardnerbuttean (earliest subage of the Bridgerian) and early middle Eocene (ca. 50 ma; Woodburne, 1987), a biostratigraphic age indicated by the co-occurrence of *Washakius* n. sp., *Palaeictops* sp. cf. *P. bridgeri* and *Palaeosyops borealis*. Other mammals known from this locality include *Didelphodus*, *Scenopagus*, *Microsyops*, *Phenacolemur*, cf. *Co-*

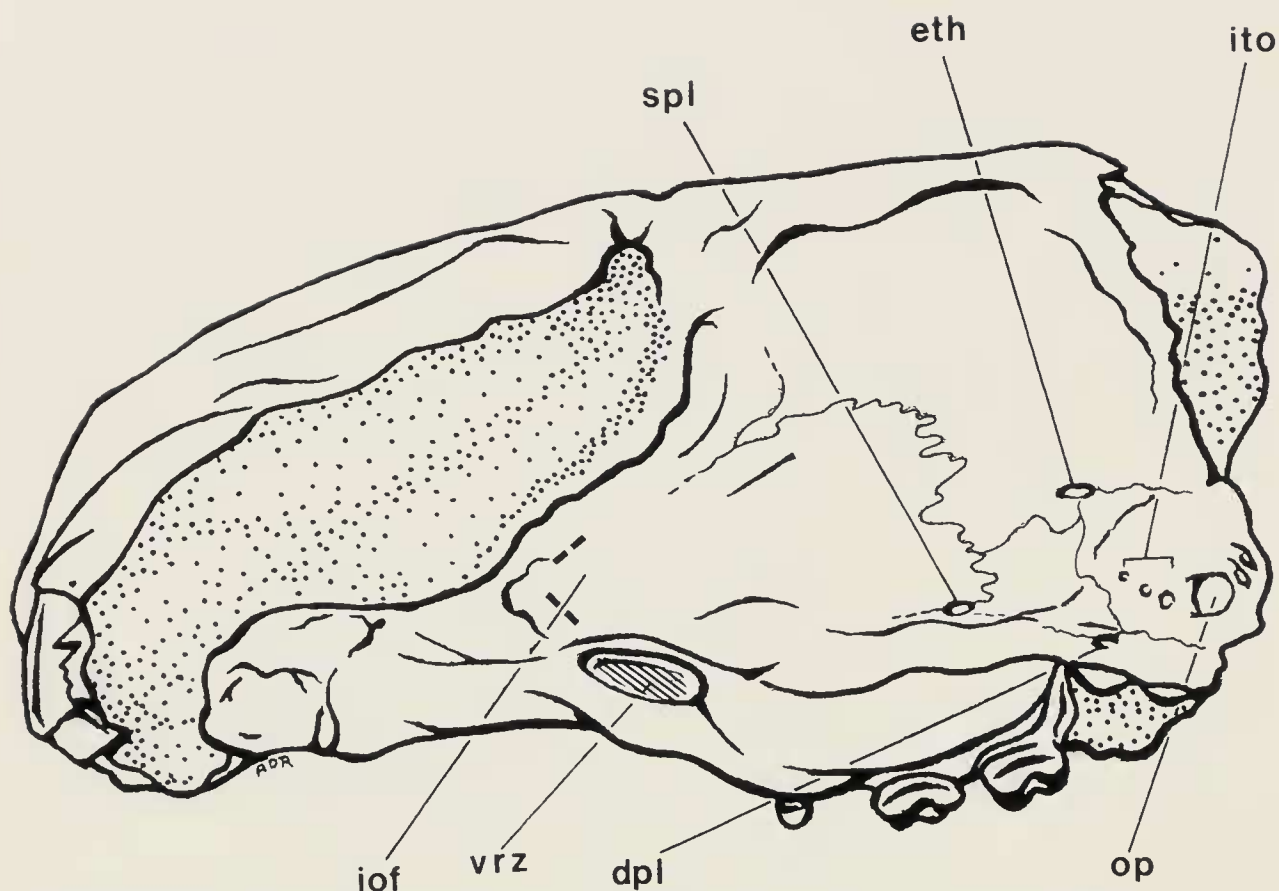


Fig. 1.—Left lateral view of rostrum, *Armintomys tullbergi*, CM 47220. Abbreviations are: dpl, dorsal palatine foramen; eth, ethmoid foramen; iof, infraorbital foramen; ito, interorbital foramen; op, optic foramen; spl, sphenopalatine foramen; vrz, ventral root of zygoma. Dashed lines mark boundaries of infraorbital foramen. Heavy line below stippled area indicates broken edge.

pelemur, *Viverravus*, *Miacis*, *Hyopsodus*, *Hyracotherium*, *Diacodexis*, and *Paramys*.

Diagnosis.—As for genus.

Etymology.—*tullbergi*, for Tycho Tullberg, in honor of his peerless studies of rodents.

Description.—CM 47220 consists of the anterior part of the skull back to about the middle of the frontal bones; a separate fragment contains the left premaxilla with the incisor and part of the left maxilla. The nasal bones and all but the anterior roots of the zygomatic arches are missing.

Distinctive features of this skull occur on the relatively long and deep rostrum. Rostral length is reflected in the ratio of P^3 - M^2 alveolar length to diastema length, which is 0.56 in *Armintomys*, compared to 0.75 in *Paramys delicatus* and 0.87 in *Sciuravus nitidus*. The premaxilla has numerous nutritive foramina dorsally and some laterally, as does the dorsal surface of the maxilla. Although most of the zygomatic arches are broken away, the remnants show that the ventral root of the zygoma extended laterally anterior to the level of P^3 (Fig. 1). The ventral root is not vertical but oblique in its attachment, oriented anterodorsally to posteroventrally. A rounded prominence on the ventral side of the zygoma runs posterolaterally into a very slight ridge that marks the anteroventral side of the zygoma. There is no distinct process for attachment of the superficial division of the masseter lateralis, which originates along this ridge.

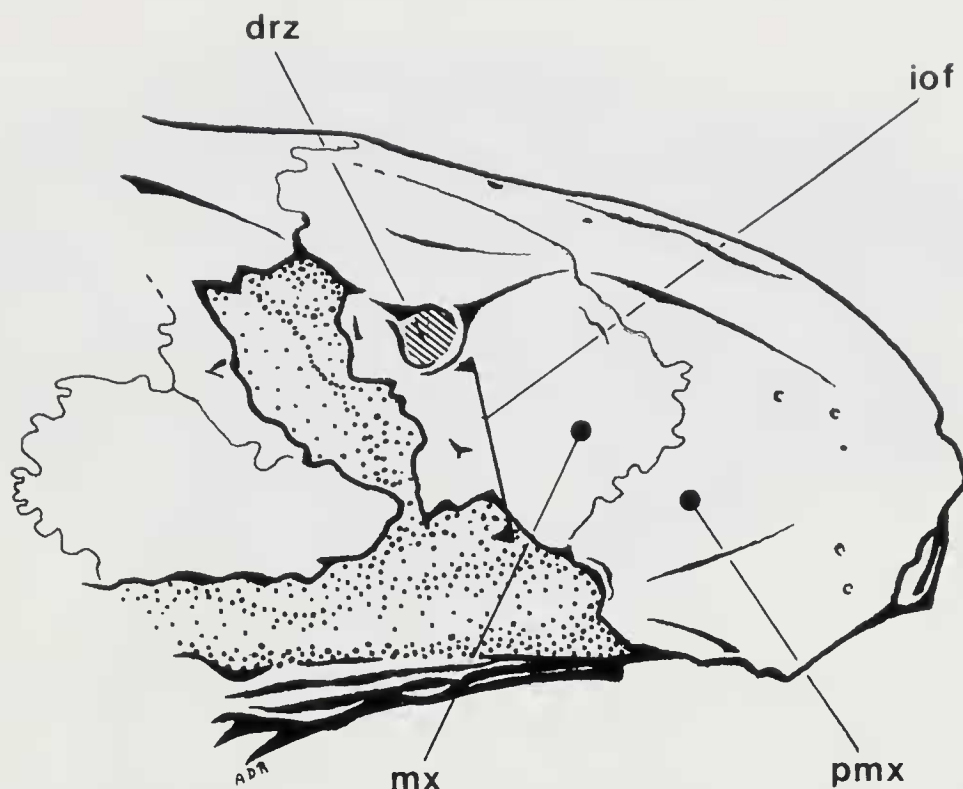


Fig. 2.—Right lateral view of rostrum, *Armintomys tullbergi*, CM 47220. Abbreviations are: pmx, premaxilla; mx, maxilla; iof, infraorbital foramen; drz, dorsal root of zygoma.

The ventral rim of the infraorbital foramen appears to have been wide transversely. The dorsal root of the zygoma is high on the side of the rostrum. A ridge extends anterodorsally from that root toward the premaxillary-maxillary suture (Fig. 2, 4). A shallow depression occurs ventral to the ridge; it extends forward from between the zygomatic roots to terminate on the premaxilla and marks the origin of the masseter medialis. This indicates a hystricomorphous condition, in which the infraorbital foramen is enlarged for passage of the masseter medialis muscle. Anterior to the zygoma there is no trace of the zygomatic “plate” that characterizes the sciuromorphic and myomorphic zygomatic structure.

Dorsally, the maxillary-frontal suture is deeply serrated; the suture is not distinct laterally but may extend anteroventrally to the dorsal root of the zygoma (Fig. 3). The frontal protrudes slightly near the anterior rim of the orbit, suggesting a weakly developed postorbital process; posterior to the process the skull narrows and then expands again to the posterior wall of the orbit. Excellent preparation revealed a number of foramina within the orbit, although not all sutures are readily discernible. In the orbital wall, the frontal extends ventrally to meet the maxilla, palatine, and orbitosphenoid bones. The lachrymal bone is not evident. The infraorbital foramen is large, as described above; there seems to be no separate neurovascular canal in the anteroventral corner of the foramen.

The anterior alveolar foramen (terminology follows Wahlert, 1974) enters the maxilla in the floor of the orbit in line with the anterodorsal edge of the ventral zygomatic root. The palatine bone rises relatively high on the orbital wall. The sphenopalatine foramen occurs at the anterior edge of the maxillary-palatine suture above the talon of M^1 . This is slightly more anterior than the condition in *Sciuravus*, and is presumably more derived (Wahlert, 1985:321). The dorsal pal-

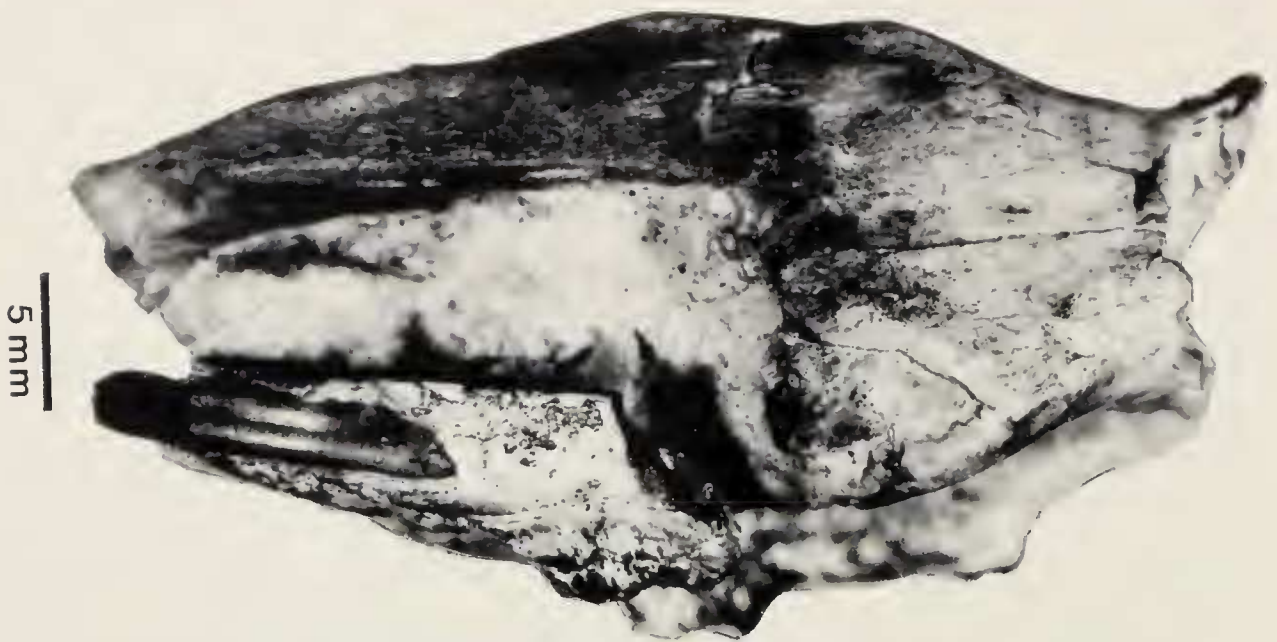


Fig. 3. — Dorsal view of skull, *Armintomys tullbergi*, CM 47220; broken left premaxilla-maxilla restored to position.

atine foramen is on the same suture above the trigon of M^3 . The relatively large, elongate ethmoid foramen perforates the frontal-orbitosphenoid suture. The transversely confluent optic foramina (0.95 mm dorsoventrally) open posteriorly into the braincase and are posterior to the level of M^3 , as in *Paramys*, which is a presumably primitive position. Anterior to the left optic foramen there are two foramina, probably interorbital; on the right there is only one. Posterolateral to the optic foramen are two small foramina, possibly for the internal ophthalmic artery. Whether these are in the orbitosphenoid or alisphenoid is not clear; on the right side there seems to be a suture marking the alisphenoid-orbitosphenoid juncture, but this is not evident on the left side.

On the palate, the incisive foramina are tear-drop shaped with the posterior end slightly wider; each is 4.0 mm long. The ratio of length of incisive foramen to length of diastema is 0.35, which is less than in *Paramys*, *Reithroparamys*, and *Sciuravus*, but greater than in *Ischyrotomus* and *Ischyromys* (Wahlert, 1974). The relatively short length of the incisive foramen may reflect the proportionately longer rostrum in *Armintomys*.

The premaxillary-maxillary suture runs down the rostrum posterior to the foramina, and extends forward to intersect the incisive foramen anterior to its end, the primitive position (Wahlert, 1985:314). The maxillary-palatine suture arches forward to about the middle of the alveolus of P^4 . The posterior palatine foramen is elongate and aligned with the trigon of M^2 . The posterior end of the palatine bone is ridged transversely and about in line with the posterior edge of the alveolus of M^3 .

Both upper incisors are preserved, though their occlusal ends are broken. Each incisor (W, 1.6 mm) has a wide, shallow groove at about the mid-line of its flattened anterior face. The enamel that covers the anterior face of the incisor extends about one-third of the way up the lateral side and curves around onto the medial wall for a very short distance. The incisor enamel, viewed with a scanning electron microscope, is pauciserial that is almost uniserial; the Hunter-



Fig. 4.—Right lateral view of skull, *Armintomys tullbergi*, CM 47220.

Schreger bands appear to be one and two prisms wide (Wahlert, personal communication, 1987).

Preserved cheek teeth are left P^3 , M^1 and M^2 (P^3 - M^2 alveolar length, 7.3 mm; Fig. 5). P^3 (L, 0.7 mm; W, 0.8 mm) is small and peg-like, with a single, flattened wear facet that faces posteriorly. The alveolus for P^4 (L, 1.5 mm) indicates that this tooth was anteroposteriorly short; it appears to have had one lingual root and two buccal roots, of which the anterior was the larger. M^1 (L, 2.3 mm; W, 2.24 mm) and M^2 (L, 2.45 mm; W, 2.4 mm) are generally similar in morphology. Each is longer than wide, but M^2 is slightly wider and M^1 is relatively longer. On both molars the four main cusps are well developed and rounded. The protocone lines up slightly posterior to the paracone, but the metacone and hypocone are aligned transversely. Viewed lingually, the hypocone is somewhat smaller than the protocone, and a valley occurs between the two cusps at the stage of wear exhibited by CM 47220. There is a small, discrete mesostyle. The prominent anterior cingulum extends from the paracone to about the middle of the protocone. The protoloph is relatively straight, and bears no suggestion of conules. The metaloph is bipartite; one part extends anteriorly and buccally from the hypocone and meets the second part extending anteriorly and lingually from the metacone. There is no development of conules on the metaloph of M^2 , but on M^1 two rounded areas, the more lingual of which is larger, may represent small conules. The posterior cingulum extends from about the midpoint of the metacone nearly to the lingual wall. Distinct wear facets occur on the antero- and posterolingual faces of the protocone and hypocone.

Discussion.—*Armintomys tullbergi* possesses a unique suite of characters that combines relatively primitive features of the cheek teeth and arrangement of cranial foramina with derived states in the structure of the incisor and zygomaseteric region. As such, the most fruitful comparisons to other rodents involve aspects of the cheek teeth and those of zygomaseteric structure and incisor enamel.

The dentition of *Armintomys* most closely resembles that of sciuravids, a family of North American Eocene rodents, in bearing a prominent hypocone on the upper molars (Wilson, 1938; Dawson, 1961). But, unlike known sciuravids, the hypocone in *Armintomys* is less well developed and the molars are longer than wide. Also, sciuravids have pauciserial incisor enamel and are not hystricomorphous, unless *Prolapsus* (see below) is a sciuravid.

One maxilla referred tentatively to the Sciuravidae (AMNH 12118; Dawson, 1962) has a small P^4 , as seems to be the case in *Armintomys*, but it differs in having a larger P^3 , molars wider than long, and a stronger molar hypocone and loph. AMNH 12118 shows no indication of hystricomorphy, although it is incomplete enough in the rostral region to leave room for doubt. Finally, in *Sciuravus? rarus* (Wilson, 1938), known from a fragmentary lower jaw with P_4 - M_1 (YPM 10729), the proportions of small P_4 and relatively elongated M_1 are somewhat similar to P^4 / M^1 proportions in *Armintomys*. Other comparisons between the partial skull of the Gardnerbuttean *Armintomys* and the partial lower jaw of the probably late Bridgerian *S.? rarus* are pointless.

The skull of the hystricognathous *Prolapsus* from the late Bridgerian of Texas has not been described in detail; it is considered to have a large infraorbital foramen that did not, however, contain the masseter medialis muscle (Wood, 1977, 1985). *Prolapsus* resembles *Sciuravus* dentally, but its incisor enamel is pauciserial to multiserial (Wood, 1985: fig. 1), which differs significantly from



Fig. 5.—Occlusal view of left upper P³, upper M¹⁻², *Armintomys tullbergi*, CM 47220.

either the pauciserial condition in *Sciuravus* or the pauciserial toward uniserial state in *Armintomys*. *Prolapsus* also differs from *Armintomys* in having larger premolars and molars that are wider than long. *Prolapsus* was most recently allocated to the infraorder Franimorpha (Wood, 1985), a generally primitive group of rodents having at least incipient hystricognathy.

Another North American Eocene hystricomorph is *Protoptychus*, a Uintan rodent with pauciserial incisor enamel; its strongly lophate cheek teeth have a persistently open buccal valley and seem to be cylindrodontid-like. A depressed area for the attachment of the masseter medialis muscle occurs anterior and dorsal to the greatly enlarged infraorbital foramen in *Protoptychus*, which differs in shape and morphological detail from that in *Armintomys*. Other differences from *Armintomys* include the relatively shorter, lower rostrum and the more posterior position of the incisive foramina. The lower jaw of *Protoptychus* has been reported as being hystricognathous (Wahlert, 1973), but the specimen requires further preparation to be certain (Wahlert, personal communication, 1990).

There is no agreement on the primitive condition of rodent incisor enamel. Sahni (1985) says it is pauciserial, but von Koenigswald (1985) and Wahlert (1989) consider multiserial enamel to be primitive. As Wahlert (1989) notes, the structural progression from multiserial to pauciserial to uniserial is a logical morphologic sequence, but, thus far, the stratigraphic evidence has contradicted logic: the oldest known condition in rodents is pauciserial. There is consensus that uniserial enamel was derived several times in parallel from the pauciserial type. Thus, *Armintomys* is best compared to rodents that are hystricomorphous and have uniserial enamel, namely, theridomorphs, anomalurids and myomorphs. The many hystricomorphous rodents with multiserial enamel (including the Eurasian

ctenodactyloids, the African phiomorphs, and the South American caviomorphs) need not be considered here.

The oldest European Paleogene theridomorphs are protrogomorphous, but their transition to hystricomorphy occurred by the late Eocene, or Robiacian (Hartenberger, 1968, 1969; Wood, 1974). The evolution in some theridomorphs from pauciserial to uniserial incisor enamel occurred by the end of the Eocene or beginning of the Oligocene. Theridomorphs have lost P^3 and have a large, quadrate P^4 . Their cheek tooth pattern is lophate (becoming highly so in some lineages), with a derived connection of the metaloph to the posterior cingulum. *Armintomys* differs markedly from the theridomorphs in dental formula, the reduced size of P^4 , and molar pattern.

The Anomaluridae, another family combining hystricomorphous zygomassteric structure and uniserial incisor enamel, was recently reported from the early Eocene in North Africa (Hartenberger *et al.*, 1985), but the material is not yet described. The earliest described anomalurids, from the late Eocene of Africa (Jaeger *et al.*, 1985), have complex pentalphodont cheek teeth that bear no similarity to those of *Armintomys*. Previous suggestions of an anomalurid-theridomorph relationship (Jaeger *et al.*, 1985 and references therein) seem reasonable.

Finally, the muroid-dipodoid rodents, the Myomorpha or Myodonta of various authors, have uniserial incisor enamel. Dipodoids are hystricomorphous, but also have a small separate neurovascular foramen anteromedial to the infraorbital foramen (Klingener, 1964). The dipodoid dentition usually includes a small peg-like P^4 , and three upper and lower molars that are anteroposteriorly elongate. Some early muroids are hystricomorphous (Lindsay, 1977); the transition to myomorphy has been documented in one lineage (Vianey-Liaud, 1974). Living muroids are myomorphous, with an infraorbital foramen constricted ventrally and with at least some development of a zygomatic plate. Muroids lack premolars.

CONCLUSIONS

The combination in *Armintomys* of a relatively primitive molar pattern reminiscent of that of sciuravids with more derived characters, including some premolar reduction, hystricomorphy, and pauciserial towards uniserial incisor enamel, occurs in no other known rodent. Any two of these characters together could represent another expression of the parallelism that is so characteristic of evolution in the Rodentia. The entire suite of features, however, especially the distribution of derived characters, strongly suggests that *Armintomys* is the earliest and most primitive known dipodoid; all other dipodoids differ from and are more derived than *Armintomys* in having a more reduced premolar dentition and a more complex, lophate molar pattern.

Discussions concerning the origin of the muroid-dipodoid group (Wilson, 1949; Lindsay, 1977; Emry, 1981) have most recently focused on two North American rodents, the Uintan to Duchesnean *Simimys* and the Chadronian *Nonomys*. Both genera appear to be hystricomorphs with a dipodoid-like separate neurovascular canal. Both lack premolars. *Nonomys* has been referred to the Muroidea on the basis of its reduced muroid dental formula (Emry, 1981). *Simimys*, in spite of its reduced dental formula, has most recently been included in the Dipodoidea, possibly as a separate zapodid subfamily Simimyinae (Emry and Korth, 1989).

Another early record of the muroid-dipodoid group is a tooth from the late

Eocene River Section of Shanxi Province, China, assigned to ?*Parasminthus* in the family Zapodidae (Hartenberger, 1975). Still more recently, Emry and Korth (1989) described the genus *Elymys*, a small rodent from the middle Eocene of North America, as a possible zapodid. *Elymys* has a relatively primitive molar pattern but exhibits the dipodoid upper cheek tooth formula of a peg-like P^4 and three molars. Not enough is known of *Elymys* to establish the nature of its zygomatic structure or incisor enamel. *Armintomys* differs from *Elymys* in having the complete rodent tooth formula, but shares with it molar characters of antero-posterior elongation, prominent hypocone, and well-developed anterior and posterior cingula. By themselves, these dental characters in *Armintomys* would not be sufficient to imply dipodoid affinity. What does warrant its referral to Dipodoidea is the combination in *Armintomys* of hystricomorphy, incisor enamel that is pauciserial tending toward uniserial, and a dentition that is not inconsistent with dipodoid affinities.

Dental evidence suggests that *Armintomys* may be derived from the sciuravids, a family previously allied with the muroid-dipodoid group (Wilson, 1949:120–122). Thus, *Armintomys*, with its hystricomorphy and altered incisor enamel, is a morphological and perhaps phylogenetic intermediate between sciuravids and dipodoids. If this interpretation is correct, *Armintomys* extends the Eocene record of dipodoids to the earliest Bridgerian. The slightly younger *Elymys* is much more advanced in dental characters. If either or both assignments of these Bridgerian rodents to the Dipodoidea stand the test of further discoveries, they will corroborate the suggestion by Wang (1985), following a study of early Oligocene zapodids from China, that the origin and radiation of dipodoids occurred considerably before the Bridgerian.

Hystricomorphy, clearly an important functional character in rodent evolution, has developed independently in at least six lineages: ctenodactylids; theridomorphs, possibly including the anomalurids; pedetids (if they are not members of another hystricomorphous, sciurognathous group); the hystricomorphous hystricognaths (assuming one origin); *Protoptychus*; and the muroid-dipodoid group. *Armintomys* may be the earliest known muroid-dipodoid rodent to express this character.

Armintomys is an example of the co-evolution of two characters linked to improved mastication: hystricomorphy and development of uniserial incisor enamel. In *Armintomys*, the former has seemingly progressed further than the latter. This is the reverse of the condition in the presumed primitive squirrel, *Protosciurus*, which retains the primitive protrogomorphous zygomatic structure but has attained fully uniserial incisor enamel (Emry and Thorington, 1982). In this character complex, as in many other aspects of their evolution, the pattern of morphologic change in rodents appears to have been mosaic and parallel.

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